

Research Article

Presence of *Palaemon macrodactylus* in a European estuary: evidence for a successful invasion of the Gironde (SW France)

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Abstract

Palaemon macrodactylus, an exotic shrimp native to the northwest Pacific Ocean, has been recorded in many estuaries along the Atlantic coast of Europe since the late 1990's. In this study, a regular monthly survey, held since 1992 of the middle section of the Gironde estuary, revealed this species' rapid and full colonization of the system since its appearance in samples during summer 1998. In the Gironde, the population of *P. macrodactylus* is self-sustaining and the species is now established there. Our study highlights two important elements that might explain its successful colonization: its ability to quickly invade a niche under-exploited by the similar native species and its greater reproductive output. The species' spatio-temporal distribution in relation to environmental variables was studied and compared with that of the native species *P. longirostris*. The exotic species was shown to mainly inhabit the polyhaline and mesohaline section of the estuary, which are sections generally under-exploited by females of the native species. Furthermore, fecundity analysis and larval abundance survey results revealed a higher potential fecundity and a greater proportion of larvae and juvenile stages for *P. macrodactylus* in the natural environment.

Key words: Invasion; interaction; *Palaemon macrodactylus*; *Palaemon longirostris*; life history traits; estuary

Introduction

Estuaries are among the most exposed systems to biological invasions; about one species in five would be non-native in European estuaries (e.g. Gollasch 2006; Reise et al. 2006; Ruiz et al. 1997; Ruiz et al. 1999). The invasibility of estuaries is explained by several factors: naturally low species richness due to the harshness of the physical environment, isolation of these systems from one another and their short existence in terms of geological time (Hedgepeth 1957), and exposure to strong anthropogenic disturbances (Reise et al. 2006; Vitousek et al. 1997). Indeed, most estuaries are sites of human activity, which favour introductions of non-native species, particularly by ship ballast waters, but in turn are also vulnerable to pollution and numerous modifications of habitat

(e.g. Grousset et al. 1999; Mc Lusky and Elliott 2004; Vasconcelos et al. 2007).

Invasive species are one of the current major environmental concerns: they are considered as a significant component of the global change and as one of the most important threats to the aquatic systems, especially because of their generally irreversible and unmanageable character (Gollasch 2006; Ruiz et al. 1997; Simberloff and Stiling 1996; Vitousek et al. 1997). The population biology of invasive species, their life history traits and ecology, should be better known to understand mechanisms and characteristics involved in the successful process of invasion (Crawley 1987; Sakai et al. 2001). The increase in these type of studies would allow us to predict the invasibility of systems and pinpoint which species are the most predisposed to invade such type of system

(Sakai et al. 2001). Invasive species can interact directly (e.g. predation, competition, parasitism) or indirectly (e.g. habitat disturbances, cascading trophic interactions) with the natives species (Sakai et al. 2001).

Benthic invertebrates account for more than half of the exotic species recorded in European coastal waters (Gollasch 2006). *Palaemon macrondactylus* Rathbun, 1902 is a suprabenthic shrimp which is native to Asian coast (Kubo 1942; Rathbun 1902). Introduced first in the San Francisco Bay of California in the 1950s (Newman 1963), this shrimp was recorded in several estuaries worldwide, in Australia (Buckworth 1979), more recently in Argentina (Spivak et al. 2006), in the Black Sea (Micu and Nă 2009; St. Raykov et al. 2010), in North America (Warkentine and Rachlin 2010), and in numerous estuaries of the European Atlantic coast (Ashelby et al. 2004; Béguer et al. 2007a; Chicharro et al. 2009; Cuesta et al. 2004; d'Udekem d'Acoz et al. 2005). The studies, which have enough data, showed well-established populations, for instance in the Guadalquivir (González-Ortegón et al. 2010). Some elements of the ecology and biology of this species were very well-studied in its area of origin, for example reproduction parameters (Fisher and Clark 1983; Omori and Chida 1988a, b). In its introduction area, its osmoregulatory capacity (Born 1968; Gonzalez-Ortegon et al. 2006) and its diet were particularly studied (González-Ortegón and Cuesta 2006; Siegfried 1982; Sitts and Knight 1979). On the other hand, any knowledge about the European populations remains very weak; the only known detailed European study of its abundance progress, its feeding habits, and its oxygen consumption patterns was carried out in the Guadalquivir population, Spain (González-Ortegón et al. 2010).

In the Gironde estuary, the first specimens of *P. macrondactylus* were identified only in 2006 (Béguer et al. 2007a). This estuary is the largest of the European Atlantic coast, with an area of about 635 km² (Figure 1). It is a macrotidal estuary, also characterized by strong turbidity and a zone of maximum turbidity which moves according to the hydraulic regime (Sottolichio and Castaing 1999). For several years, the Gironde estuary has been under various anthropological pressures likely to alter or to have altered its functioning (Mauvais and Guillaud 1994): these include a nuclear power plant, an active harbour with associated

important dredging activity, fisheries and an intensive viticulture industry which causes organic pollution (Budzinsky et al. 1997).

Until the discovery of *P. macrondactylus*, only two shrimp species were identified as common and abundant in the Gironde estuary: the brown shrimp *Crangon crangon* Linnaeus, 1758, a marine species which enter the estuary mainly at juveniles stages, and *Palaemon longirostris* H. Milne Edwards, 1837, a resident species typical of estuaries (Aurousseau 1984; Girardin et al. 2008; Sorbe 1983). *P. macrondactylus* is very similar morphologically to *P. longirostris*, and consequently the invader remained unnoticed for several years after it was introduced (Ashelby et al. 2004; González-Ortegón and Cuesta 2006). Moreover, their ecology seems similar (osmoregulatory capacity, diet) and an interaction between both species is very likely (Béguer et al. 2007a; González-Ortegón et al. 2010). Thus, like in Great Britain, *P. longirostris* could be considered of important conservative value in the Gironde (Chadd and Extence 2004). Indeed, *P. longirostris* has a strong socio-economic value (it represents about 11% in weight and 7% in value of the Gironde fishery landings) and is also a key species in the estuarine trophic network (Lobry et al. 2008).

The first objective of this study was to determine if *P. macrondactylus* represents, at present, a well-established population in the Gironde. The state of its population and its progression of colonization were determined on the basis of regular monthly surveys conducted since 1992 and compared with those of the native shrimp *P. longirostris*.

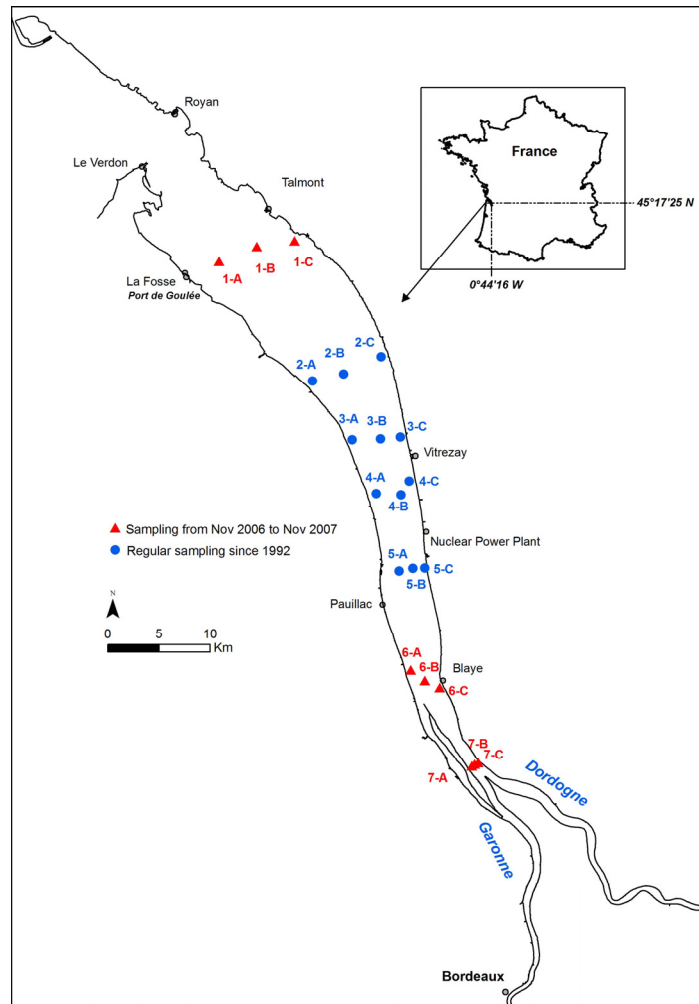
The second objective was to test two hypotheses which might explain the species's successful colonization of the Gironde: (i) *P. macrondactylus* exploits niches seldom used by the native species, and (ii) it has a higher reproductive potential than the native *P. longirostris*.

Materials and methods

Density surveys

Since 1992, a large part of the estuary has been sampled monthly for power plant surveillance monitoring through faunal survey, mainly fishes and crustaceans, through 4 transverse transects spread over a 20-km-long section (Girardin et al. 2008) (Figure 1 and Appendices 1–3). Each

Figure 1. The sampling stations in the Gironde estuary (for geographic coordinates and environmental information see Appendices 1–3).



transect has 3 stations, each one being sampled at the bottom and at the surface. The water surface was sampled using two push-nets located on each side of the boat (section 4m × 1m, stretched mesh of 1 mm at the end). The bottom was sampled using an Agassiz trawl consisting of a metal frame 2 m × 1.2 m kept at 0.2 m from the bottom by skates with similar mesh size. Sampling was carried out only during daytime between the mid-flow and the slack period of the high tide in order to minimize possible density variations related to the tide. Each tow lasted about seven minutes. Classical physical parameters were noted at each station (water temperature, salinity and turbidity). Flowmeters (Generals Oceanics) fixed at the entry of each net, allowed to calculate the

volume of filtered water during each sampling. Captures were transformed to density and expressed as number of individuals collected by 1000m³ water filtered. On average, the volume of filtered water was 1238m³ for each bottom station and 2460m³ for each surface station. All sampled organisms were preserved in formalin and stored in plastic containers. Since the presence of *Palaemon macrodactylus* was detected only in 2006, we re-examined stored samples to provide a retrospective analysis of its introduction and progression. A preliminary study revealed its first known occurrence in August 1998 (Béguer et al. 2007a) and only in very low numbers from then until 2002. To assess its progress over time, a random sub-sample of the previously collected samples from

1998 to 2002 were reanalyzed. Finally, 90% of the samples of 2003, 66% of 2004, 67% of 2005 and 86% of 2006 were examined again.

Additional to the previous monthly survey, an extended survey was carried out monthly across a 60-km-long section of the estuary between November 2006 and November 2007, using the same protocol (Figure 1, 3 additional transects). In order to assess the presence of shrimp larvae, a plankton net (1.1m in diameter, 4.5m in length, mesh size of 200 μ m) was used for surface sampling. The net was lightly weighted, and was towed by the boat very slowly, against the current, for about 1 minute. The filtered volume was around 38m³ at each sampling station, from the top 1 meter of surface water. The samples were stored in 70° alcohol.

Temperature, salinity and turbidity were recorded at each station with a multi-parameter probe IDROMAR IM51-IM201. During the survey, temperature ranged between 8.0 and 22.8°C (mean = 15.7°C), salinity between 0 to 27 PSU (mean = 8.2 PSU) and turbidity between 56 to 4000 NTU (mean = 1400 NTU). Temperature varies only according to the month, whereas salinity and turbidity vary according to the station and the month (tide and river flows).

Reproductive parameters

To assess the breeding period, we distinguished between ovigerous and non ovigerous shrimp (by the presence of eggs) in subsamples of each sample collected between November 2006 and November 2007. About 30 individuals from each bottom station were haphazardly picked out, representing about 126 shrimps per month for a total of 1509 *Palaemon macrodactylus*. Sex was determined by recording the presence or absence of the *appendix masculina* on the endopod of the second pleopod, which is a male attribute. To assess the size at onset of sexual maturity (SOM) for females, the method used was based on morphometric characteristics, assuming that changes in the allometric growth of the pleura are related to the development of the brood chamber found in breeding females (Omori and Chida 1988b; Teissier 1960). This is the best known and most frequently used method in studies of SOM for female crustaceans (Lizarraga-Cubedo et al. 2008). Thus, both cephalothorax length (CL, from the base of eyestalk to the posterior edge of cephalothorax) and pleura maximum width (PL, second abdominal segment) were measured to the

nearest 0.01 mm under a stereomicroscope, with the aid of a micrometer, on 316 females. The total length (TL, without the rostrum) was also measured on 411 individuals (males and females). To assess body condition, 1007 individuals were weighed to the nearest milligram after a few days of storage in alcohol (Wf, this weight was assumed to be the fresh weight).

Fecundity analysis was done on a total of 178 *P. macrodactylus* females and 303 *P. longirostris* partitioned from 2003 to 2007. According to a previous study where the spatial and temporal variability of *P. longirostris* fecundity was assessed (Béguer et al. 2010a), females were haphazardly picked out from stations where they were the most abundant but from similar months for each year (i.e. May or June for *P. longirostris* and June, July or August for *P. macrodactylus*).

Ovigerous females were immersed in a 10 % bleach solution in order to remove the eggs from the abdomen (Choy 1985). Eggs were counted one by one without subsampling. Embryos were classified as stage I (no visible eyes) or stage II (eyes well developed) (Corey and Reid 1991). Fecundity was expressed by the equation of number of eggs (EN) on carapace length: $EN = a CL^b$. About 50 eggs per females chosen haphazardly from both species were automatically measured using a dissecting microscope coupled to a computer with Image-Pro plus software (A.E.S). The mean diameter (mean of the longest axis and shortest axis) of 5808 eggs from 135 *P. macrodactylus* and 79 *P. longirostris* collected in 2003 and 2007 were measured.

Statistical analysis

From monthly densities of both species, we determined the trend of the relative proportion of *Palaemon macrodactylus* using a generalized linear model (binomial family, McCullagh and Nelder 1989). Morisita's original index was used to assess to the spatial overlap of both species (native and exotic) (Smith and Zaret 1982). Differences in spatial overlap between years or months were performed with Wilcoxon tests with Bonferroni correction.

The center of mass of the two populations related to the distance to the sea (D_{CM}) and to the salinity value (S_{CM}) was calculated for each sampling date according to the method used by González-Ortegón et al. (2006; 2010): $D_{CM} = \sum p_i D_i$ and $S_{CM} = \sum p_i S_i$, where p_i is the proportion of the individuals collected at the sampling i and D_i and S_i are the distance and salinity,

respectively, characterizing sample *i*. The D_{CM} and S_{CM} values were calculated for *P. longirostris* before and after introduction of *P. macrodactylus*, based on the regular survey data (20 km area), in order to assess possible changes in distribution. Statistical differences were detected using a Wilcoxon test for non-normal data. The calculated values were summarized in violin graphs which are a combination of box plot and kernel density plot.

Links between environmental factors and shrimps densities were explored using Generalized Additive Models (GAMs) (Hastie and Tibshirani 1990). A Gamma error distribution via a log link function was applied. To obtain the relative importance of the variables (predictor), we assessed the residual deviance change after excluding each variable in turn from the final model. To evaluate the model, we used its percentage of variance explained (i.e. the difference between the Null model deviance and the residual model deviance, divided by the Null model deviance). The software R was used (R Foundation Core Team 2005), with the GAM package (Hastie 2005) to perform the GAM. Presence of ovigerous females in the samples was also related to the recorded environmental variables using a GAM, but a binomial error distribution via a logistic link function was applied. To evaluate these models, the kappa coefficient, which measures the correct classification rate (proportion of correctly classified presences and absences) after the probability of chance agreement has been removed, was calculated (Landis and Koch 1977).

Linear regressions of log-transformed data were determined for pleura width (PL) on cephalothorax length (CL), for the ovigerous and non-ovigerous females separately, to assess to the SOM – Size at onset of sexual maturity. The comparison between the two log-transformed regression lines was carried out using an analysis of covariance. The change in relative growth of the pleura for the non-ovigerous females, was identified with the package “segmented” in R (Somerton 1980; Davies 1987). Given the linear model $\log PL \sim \log CL$, the Davies' test tests for a non-zero difference-in-slope parameter of the segmented relationship. The procedure computes a number of naive points Wald statistics for the difference-in-slope, seeks the best value, and then corrects the selected (minimum) p-value. Non-ovigerous females from the breeding period were assigned into mature or immature category

according to the inflection point (hypothesized transition point).

Differences in fecundity between the species and for each year were explored by computing linear regressions of log-transformed data of the number of eggs against cephalothorax length. The comparison between the regression lines, taking into account embryo stage, was carried out using an analysis of covariance.

The significance threshold selected was 5% for all the tests.

Results

Abundance survey over time

On average 78.0 % (± 1.7 SE) of the shrimps were collected at the bottom. Thus, due to the paucity of surface data, only the bottom stations were considered in the rest of the study. Since its appearance in our survey area in August 1998, the density of *Palaemon macrodactylus* has varied a lot according to the season and the years (Figure 2), with a mean of 11.2 individuals $10^{-3}m^{-3}$. The peak abundance was recorded during summer 2003, with a density of 96.8 individuals $10^{-3}m^{-3}$. *P. macrodactylus* was recorded in our study area predominantly during summer and autumn; spring was the season when the recorded densities were the lowest. Since 2003, the abundance of *P. macrodactylus* has seemed to decline, but its frequency relative to the native species *P. longirostris* was still significantly increasing ($p < 0.001$). In 2007, *P. macrodactylus* represented 19.9% of the individuals collected; this proportion varied significantly between stations and seasons and may have reached 100%. In terms of fresh biomass, *P. macrodactylus* relative frequency was lower with 10.3 % on average in 2007.

Results of the morphometric analysis (length and weight) are presented in Tables 1 and 2. The *P. macrodactylus* shrimps collected were significantly smaller than *P. longirostris*, by 30% for females and 19% for males ($p < 0.001$). In both species, males were smaller than females. Within the studied area, we observed a higher proportion of juveniles in the population of the exotic species than in that of the native *P. longirostris*, with an average of $31\% \pm 26$ and $5\% \pm 7$ respectively.

A total of 1460 *Palaemon* sp. larvae were collected in 2007 (Appendix 1). These larvae were present only in the samples collected from May to September. Only a few first stages, Zoe I

Figure 2. Abundance of *Palaemon macrodactylus* in the Gironde estuary since 1992 : seasonal mean of abundance and annual mean proportion compared to the native species *P. longirostris* (bottom stations).

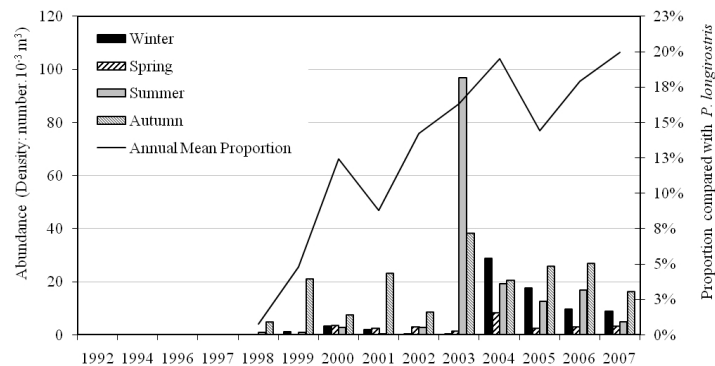
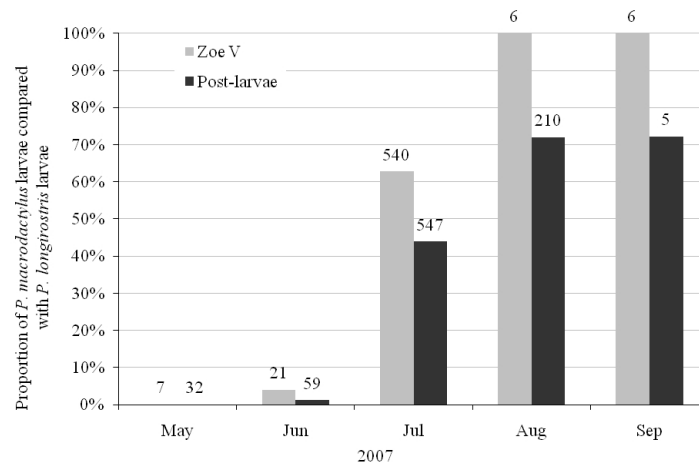


Figure 3. Relative frequency of *Palaemon macrodactylus* larvae compared with *P. longirostris* larvae collected in the first meter of water under the surface in the Gironde estuary in 2007. Numbers above histograms indicate the total number of collected larvae for both species.



to Zoe IV, were collected: 18 *P. macrodactylus* (including 14 Zoe I) and 7 *P. longirostris* (including only one Zoe I). Most of the larvae collected were stage Zoe V and Post-larvae. For both species, stages I to V were collected in the downstream part of the estuary (5-23 PSU) whereas post-larvae stages were collected in the upstream part (0-6 PSU). On average, *P. macrodactylus* represented 53% of the Zoe V stages and 38% of the post-larvae (Figure 3). The mean estimated densities were 3.5 Zoe V larvae for 50 m³ and 2.3 post-larvae for 50 m³. The maximal density recorded for *P. macrodactylus* was 225 larvae m⁻³ for Zoe V (vs 116.3 for *P. longirostris*) and 28.6 m⁻³ for post-larvae (vs 55.5 for *P. longirostris*). A time-lag in the appearance of larvae was observed: *P. longirostris* larvae were predominant at the beginning of the presence period whereas *P. macrodactylus* larvae were predominant at the end, i.e. in August and September (Figure 3).

Hypothesis 1: Palaemon macrodactylus occupies a different niche than the native species.

Since 1999, the spatial overlap between *Palaemon macrodactylus* and *P. longirostris* in our study area was strong, with a mean Morisita's original index of 0.53 (Figure 4). This index did not vary significantly through the year and the seasons ($p > 0.05$). The distribution of *P. macrodactylus* and *P. longirostris* populations were significantly different in the sampling area during the survey, when measured as distance to the sea ($p < 0.001$) and with respect to the salinity ($p < 0.001$) (Figure 5). Since its introduction, *P. macrodactylus* population was distributed farther downstream in the estuary (mean D_{CM} = 38.8 km, against 39.4 km for *P. longirostris* population). As a result, *P. macrodactylus* population inhabits more saline area than *P. longirostris*. The maximal spatial overlap occurred in the central, mesohaline part of the estuary.

Table 1. Characteristics of the individuals collected in the Gironde estuary between November 2006 and November 2007 (CL: Cephalothorax Length without rostrum; Wf: Fresh Weight, N: number of individuals measured).

		Females		Males	
		<i>P. macrodactylus</i>	<i>P. longirostris</i>	<i>P. macrodactylus</i>	<i>P. longirostris</i>
CL (mm)	Mean \pm SD	7.0 \pm 1.8	9.1 \pm 1.7	5.6 \pm 1.0	6.9 \pm 1.2
	Min-Max	3.4 - 13.1	4.0 - 14.6	3.2 - 9.5	2.6 - 10.2
Wf (mg)	Mean \pm SD	344 \pm 271	603 \pm 302	179 \pm 95	315 \pm 118
	Min-Max	38 - 1583	620-1932	29 - 629	370-3890
N		554	1384	455	2055

Table 2. Results of regressions calculated from weight and size of *Palaemon macrodactylus* sampled in the Gironde estuary in 2007, where N is the number of measured individuals.

Sex	N	Equation	R ²	p-value
Males	457	Wf= 0.0011 CL ^{2.8817}	0.90	<0.001
Non ovigerous females	440	Wf= 0.0013 CL ^{2.7502}	0.94	<0.001
Ovigerous females	110	Wf= 0.0022 CL ^{2.5567}	0.91	<0.001
All individuals	411	TL= 4.3512 CL ^{0.9056}	0.96	<0.001

The distribution of the *P. longirostris* population in the sampling area has statistically significantly changed since *P. macrodactylus* appeared, the center of mass moved upstream 0.770 km on average ($p=0.001$) and was in a less saline area at the end of the survey ($p<0.05$). The differences were observed for all seasons. In the studied area, the mean salinity has not significantly changed since the exotic species was introduced ($p>0.05$).

From November 2006 to November 2007, spatial distributions of the two *Palaemon* species were observed monthly according to sex across a large survey area (Figure 6). Both species showed different distributions according to month and from this information, migratory patterns began to emerge. For *P. macrodactylus*, the distribution and migration patterns were very similar between the sexes, only June showed different distributions. During winter, *P. macrodactylus* population was widely distributed through the estuary, its distribution covering the 60 km of the sampling area, i.e. from a distance of 14 to 74 km to the sea. From February, its distribution was more restricted and was closer to the sea, and extending outside of our survey area during summer (particularly for females). From September, its distribution became wider, covering the whole sampling area, with a more important concentration in the median part of the estuary. Differences in *P. longirostris* distri-

bution were more pronounced according to the month and the sex. Contrary to *P. macrodactylus*, *P. longirostris* females moved away from the downstream part during winter. An important concentration in the downstream part was observed in June for females, and also in May for males. Then, *P. longirostris* population went upstream and spread more downstream in autumn.

An important part of these density variations was explained by the environmental variables recorded, such as temperature, salinity and turbidity, as shown by the results of GAM summarized in Table 3. Differences between species were revealed, particularly with the salinity. Response curves to salinity were similar for males and females for *P. macrodactylus* (i.e. bell-shaped with a maximum around 11–17, whereas densities of females *P. longirostris* decreased with salinity and densities of males showed a maximum around 9–12 PSU) (Figure 7). Responses to turbidity were unidirectional and similar for both sexes: densities increased with turbidity. However densities increased up to a threshold of approximately 2000 NTU for *P. macrodactylus* whereas the response was more linear for *P. longirostris*. Response to temperature (the most important factor for *P. macrodactylus*) was similar for both sexes and species: the abundance decreased as the temperature increased (Figure 7).

Figure 4. Annual values of Morisita's original index of spatial overlap between *Palaemon macrodactylus* and *P. longirostris* in the survey area of the Gironde estuary since 1999 (Error bars represents standard deviation).

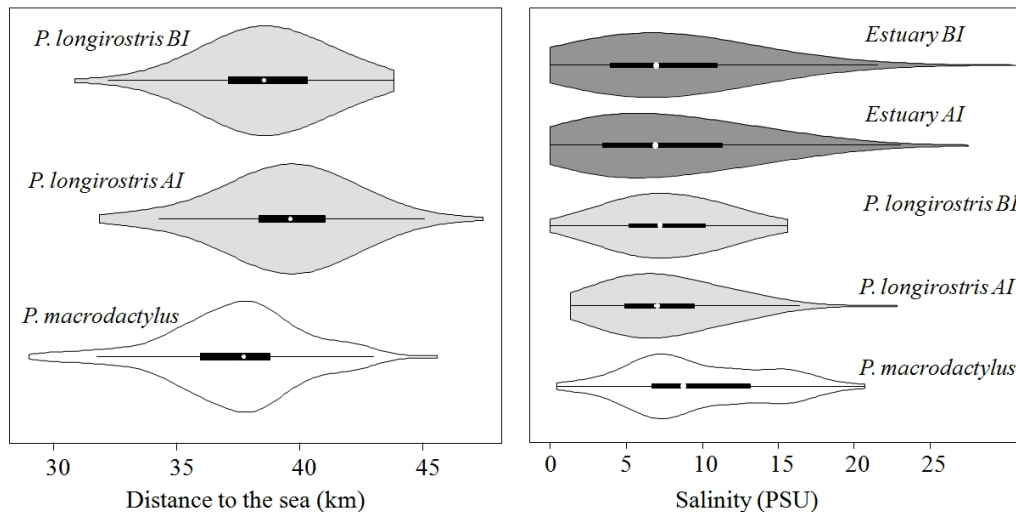
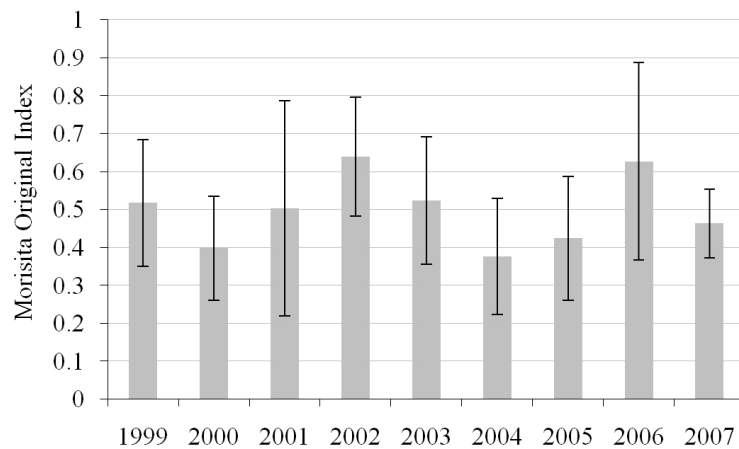


Figure 5. Violin plots of the distance (km) and salinity at which the centre of mass (D_{CM} and S_{CM}) of *Palaemon longirostris* and *P. macrodactylus* populations were situated, before introduction (BI) and after introduction (AI) of *P. macrodactylus*. The plots include a marker for the median of the data and a box indicating the interquartile range.

Hypothesis 2: Better reproductive traits for *Palaemon macrodactylus*

The breeding period is seasonal for both species but a time-lag was observed between them (Figure 8). *Palaemon macrodactylus* ovigerous females were recorded from April to September, with a peak generally in July, whereas *P. longirostris* breeding period extended from February

to August, with a peak in May or June (Figure 9). The relationship between the ovigerous female presence and the water temperature was examined with a GAM (binomial family). For both species, the breeding period was significantly linked to the increase of temperature. This environmental factor explained a more important part of the deviance for *P. macrodactylus* (46.3%, kappa = 0.57) than for *P. longirostris* (11.3%, kappa = 0.28).

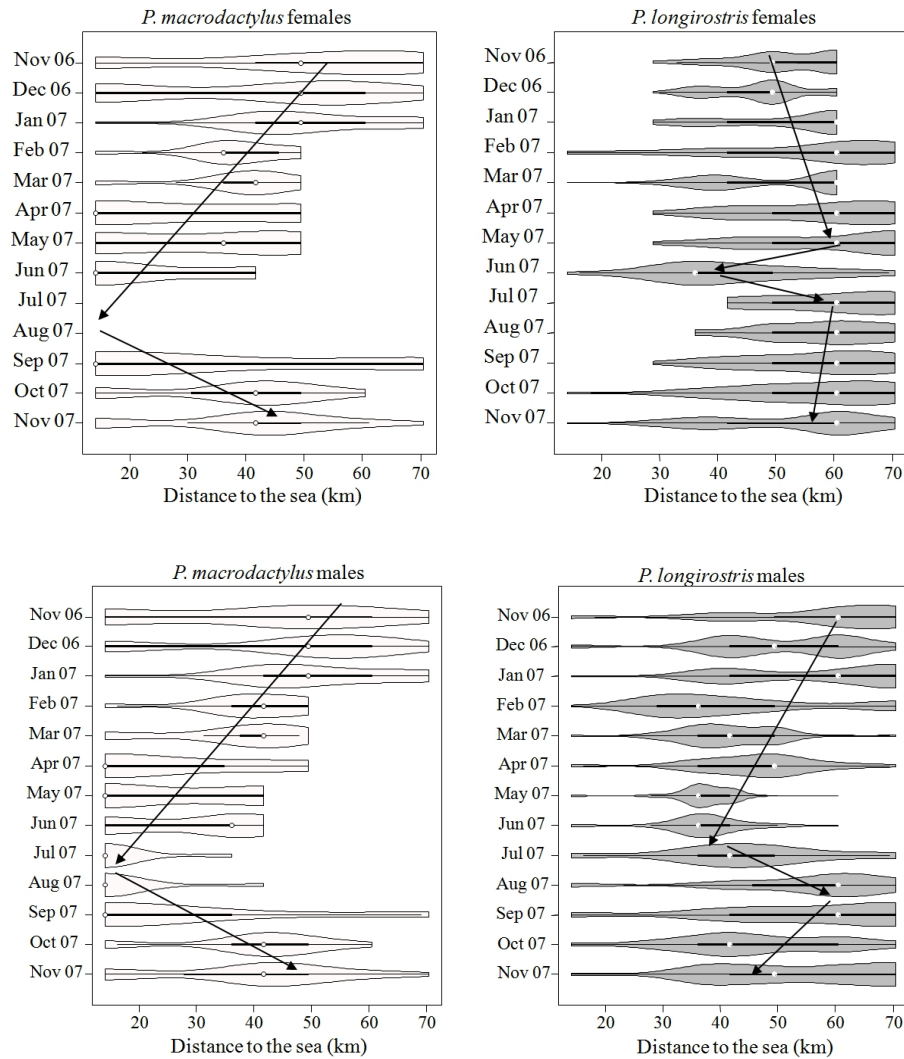


Figure 6. Violin plots of the horizontal distributions of the *Palaemon longirostris* and *P. macrodactylus* populations, observed from November 2006 to November 2007, in the Gironde estuary. The arrows symbolize the migration trend observed.

Table 3. Summary of the generalized additive models built to explain the estimated densities of the *Palaemon* populations during the extended survey (2006–2007) in the Gironde estuary. All variables are significant (threshold 5%).

Species	Sex	Rank of variables relative to their contribution to the model			Explained deviance (%)	Correlation between predicted and observed data	
		Temperature	Salinity	Turbidity		rho (Spearman)	p-value
<i>P. macrodactylus</i>	females	1	2	3	53.1	0.74	<0.001
	males	1	2	3	53.0	0.72	<0.001
<i>P. longirostris</i>	females	3	1	2	46.3	0.67	<0.001
	males	2	1	3	27.5	0.59	<0.001

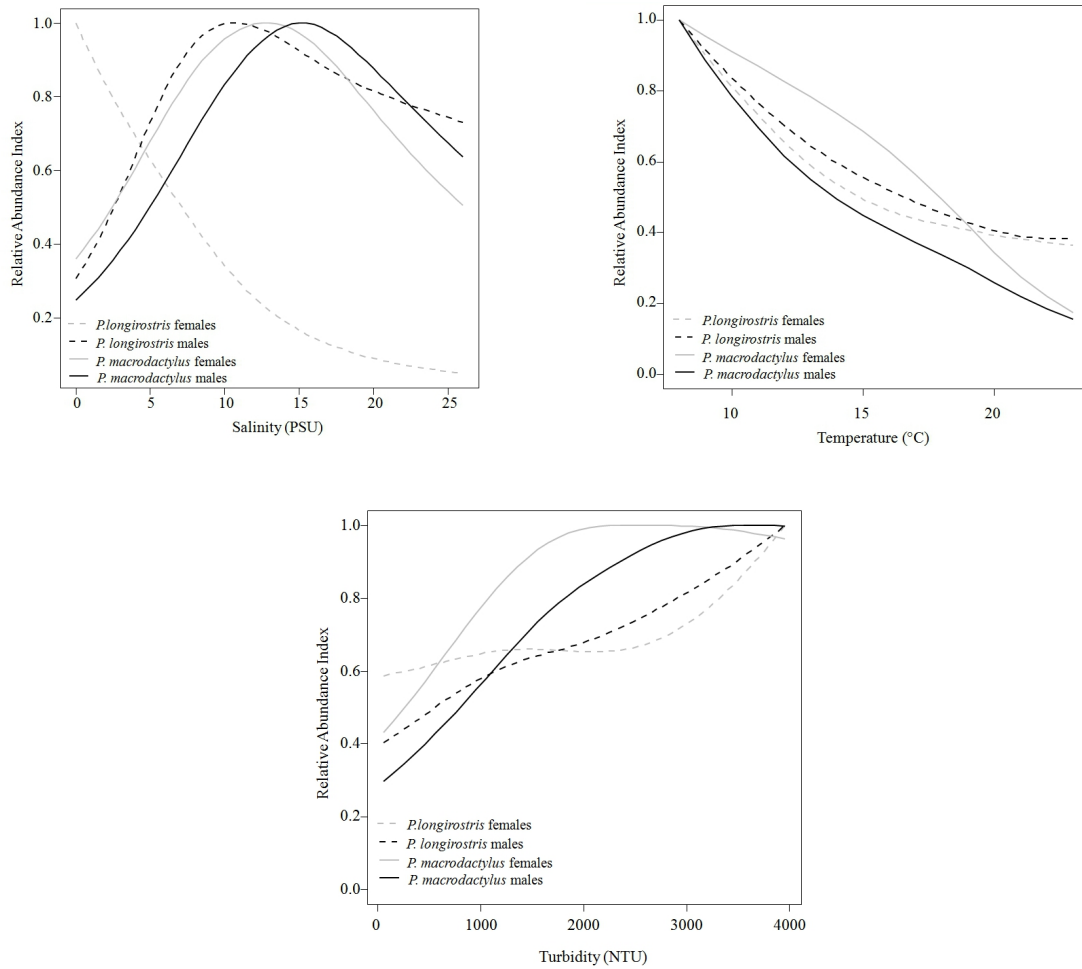


Figure 7. Mean response curves of shrimp densities to recorded environmental variables (Predicted values from GAM).

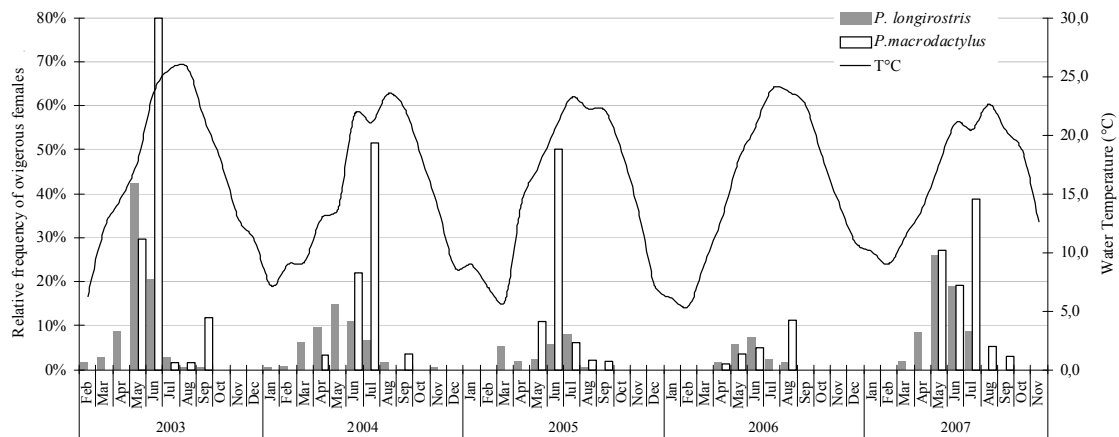


Figure 8. Comparison of the breeding period (presence of ovigerous females) between *Palaemon macrodactylus* and *P. longirostris* in the Gironde estuary since 2003.

The size at onset of sexual maturity was very similar between species: around 7.6 mm CL for *P. macrodactylus* (Figure 9) versus 8.0 for *P. longirostris* (see Bégue et al. 2010a for figure). For both species, 3 morphotypes were detected among females: young, non-ovigerous and ovigerous.

The relationship between female size and egg number was significantly different between species ($p < 0.05$): for a similar size, *P. macrodactylus* carried more eggs than *P. longirostris* (Figure 10), regardless of year. *P. macrodactylus* fecundity varied between 29 and 2090, with an average of 577 eggs per female. For *P. longirostris* fecundity varied between 78 and 1391, with an average of 529 eggs per female when all years were considered (Table 4). The number of eggs was not significantly linked to embryo stage (no visible eyes or eyes well developed) for either species.

Mean size of ovigerous females was significantly different between species; *P. longirostris* females collected being generally bigger than *P. macrodactylus* (Table 4). Size distributions of *P. macrodactylus* were similar between years, except in 2006 when sizes were significantly smaller than in other years ($p < 0.001$). *P. longirostris* sizes were significantly different each year, except in 2006 and 2007 for which distributions were similar.

P. macrodactylus eggs were significantly smaller than those of *P. longirostris* ($p < 0.001$), by 12.3 % for Zoe I and 14.3 % for Zoe II (Table 5). For each species, egg diameters were different depending on the stage. Zoe II were bigger than Zoe I, but the diameter did not differ significantly with respect to the collection year (2003 and 2007). Only in the case of Zoe II was the mean diameter of eggs significantly linked to egg number – the mean egg diameter decreasing with increasing number of eggs ($p < 0.05$).

Discussion

An established population, gaining ground on the similar native species

Our study provides strong evidence that *Palaemon macrodactylus* has become established in the Gironde estuary since its first appearance in our samples in summer 1998. The oldest samples that were reexamined (1992-1997) did not identify the presence of any exotic shrimp. This seems to be the oldest record of this species

in European waters, in addition to the Guadalquivir one (González-Ortegón et al. 2010). However, the true introduction could be older and not recorded in our sampling that covered only the middle section of the estuary. According to the various phases of invasion established by Reise et al. (2006), it seems that after a phase of establishment then an expansion until 2003, *P. macrodactylus* is currently in a phase of adjustment in the Gironde estuary. Its abundance since its introduction are not recorded as a gradual increase, contrary to the Guadalquivir population (González-Ortegón et al. 2010). Indeed, our data show a phase of very low abundances between 1998 and 2002, followed by an exceptional peak of abundance in 2003, then a gradual decrease until 2007. The peak of 2003 matches with an exceptional climatic period: the water temperature was particularly high, especially in spring and summer (summer peak of 26°C) and the intrusion of marine waters into the estuary was important. Some effects on the zooplanktonic populations were also observed: the strong abundances of copepods and mysids shifted upstream, and for some species, a seasonal peak of early abundance was observed (David et al. 2005). The strong abundances of *P. macrodactylus*, observed at the same time in our survey area, could be due to an increase of its main prey items, which are mysids and copepods (González-Ortegón et al. 2010; Siegfried 1982; Sitts and Knight 1979). This peak of abundance could also be due to a spatial shift in the distribution of the core population into our survey area from where it may be usually located, i.e. downstream. This peak could also be due to the normal exponential rise in population of successful invaders. Since 2003, the mean abundance of *P. macrodactylus* in our survey area was $16.6 \text{ individuals} \cdot 10^{-3} \text{ m}^{-3}$; the mean densities could reach $96 \text{ individuals} \cdot 10^{-3} \text{ m}^{-3}$ (summer peak of 2003). These densities seem weaker than those observed for the population of Guadalquivir ($54 \text{ individuals} \cdot 10^{-3} \text{ m}^{-3}$), also five years after their appearance in samples (González-Ortegón et al. 2010). On the other hand, they are more important than those of the Lower San Francisco Estuary where a population has been established for about fifty years (Gewant and Bollens 2005; Newman 1963). The size of the systems could explain these differences. However, the mean abundance in the Gironde could be underestimated because of our

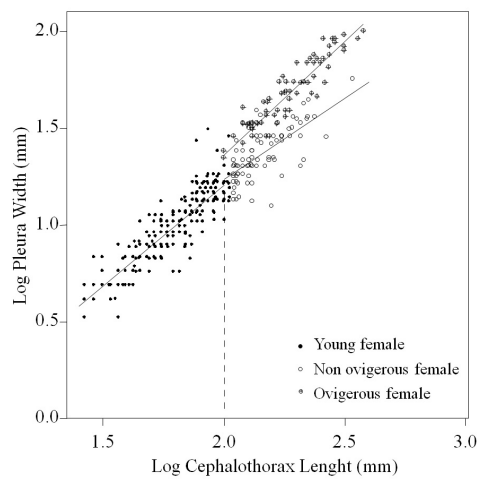


Figure 9. Allometric relationships between Pleura width and Cephalothorax length for *Palaemon macrodactylus* females in the Gironde estuary. Young female : $LP=0.128CL^{1.05}$ ($r^2=0.74$, $p<0.001$; $N=173$); Non ovigerous female : $LP=0.366CL^{0.84}$ ($r^2=0.44$, $p<0.001$; $N=78$); Ovigerous female : $LP=0.116CL^{1.15}$ ($r^2=0.83$, $p<0.001$; $N=65$).

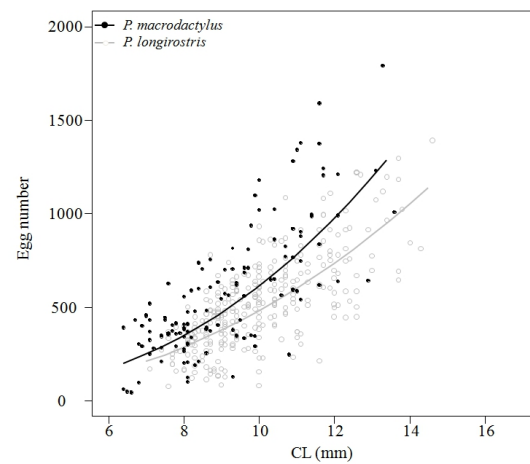


Figure 10. Relationship between egg number and female size of *Palaemon macrodactylus* and *P. longirostris* in the Gironde estuary and sampled between 2003 and 2007. *P. macrodactylus* : $EN=1.7860CL^{2.5352}$ ($r^2=0.40$, $p<0.001$; $N=177$); *P. longirostris* : $EN=2.3011CL^{2.3196}$ ($r^2=0.44$, $p=0.001$; $N=289$).

Table 4. Relationship between egg number (EN) and female size (CL) $EN = a CL^b$, with N the total number of individuals measured.

Year	<i>P. macrodactylus</i>						<i>P. longirostris</i>					
	a	b	r^2	N	Mean Egg Number, \pm SD	Mean CL (mm, \pm SD)	a	b	r^2	N	Mean Egg Number \pm SD	Mean CL (mm, \pm SD)
2003	0.686	3.0305	0.52*	35	731 \pm 426	9.5 \pm 1.5	0.7957	2.7605	0.52*	30	723 \pm 226	11.6 \pm 0.9
2005	0.1196	3.5712	0.36*	30	537 \pm 388	9.8 \pm 1.5	0.6819	2.841	0.39*	35	347 \pm 196	8.6 \pm 1.1
2006	0.0897	4.1211	0.49*	37	520 \pm 454	7.7 \pm 1.2	33.5165	1.0981	0.17**	30	447 \pm 157	10.1 \pm 1.5
2007	2.1704	2.4276	0.54*	75	545 \pm 288	9.3 \pm 1.6	1.995	2.4012	0.39*	194	547 \pm 234	10.0 \pm 1.4
All years	1.7861	2.5352	0.40*	177	577 \pm 378	9.1 \pm 1.7	2.3011	2.3196	0.42*	289	529 \pm 246	10.0 \pm 1.5

* $p<0.001$

** $p<0.01$

sampling area, which is limited to the median section of the estuary. The extended survey of 2007 showed that the *P. macrodactylus* population extends upstream or downstream of this area according to months. Furthermore, it seems that an area not usually sampled located downstream, 5 km from the the south of La Fosse (Port de Goulée, Figure 1), is particularly rich in *P. macrodactylus* (samples from commercial fisherman, 2005 and 2007, unpublished data).

Contrary to the density pattern obtained for our study area, the relative frequency of *P. macrodactylus* compared with the native species *P. longirostris* has gradually increased since 1998. In 2007, the exotic shrimp represented approximately 20% of all shrimp collected in the estuary. Its frequency compared with *P. longirostris* is lower than in the Guadalquivir where *P. macrodactylus* accounts for about half of the genus representatives (González-Ortegón et al. 2010). But in the

Table 5. Comparison of egg diameters between *Palaemon macrodactylus* (N=135 females) and *P. longirostris* (N=79 females) in the Gironde estuary (data collected in 2003 and 2007).

	Mean Egg diameter (μm) \pm SD			
	<i>P. macrodactylus</i>		<i>P. longirostris</i>	
Stage I (no visible eyes)	535 \pm 61	N = 1947	610 \pm 51	N = 757
Stage II (eyes well developed)	588 \pm 65	N = 1886	686 \pm 54	N = 604

Gironde, its frequency in the whole estuary until 2007 is considered an underestimate because of the restricted sampling area. In any case, the sustained presence of ovigerous females and the occurrence of early larval stages in samples for several recent years provide strong evidence that the Gironde population of *P. macrodactylus* is self-sustaining and the species is now naturalized (Eno et al. 1997). With the native *P. longirostris*, they are now the two only resident shrimps of this system.

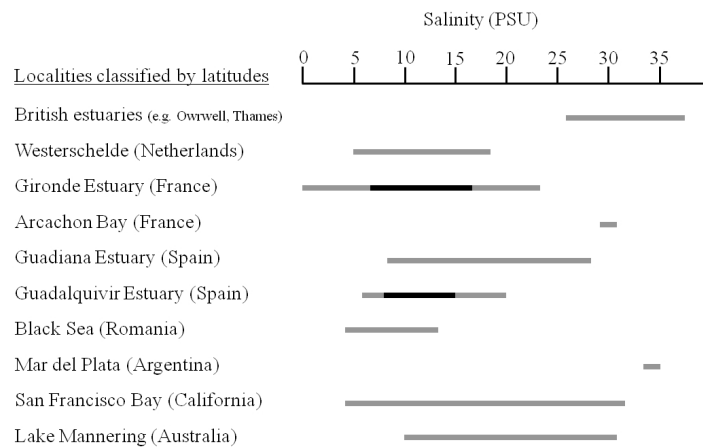
Palaemon macrodactylus is able to initially colonize areas seldom occupied by the native *P. longirostris* and eventually displace the latter

In the Gironde estuary, the center of density of the exotic population is located more downstream than that of the native species. Consequently, *Palaemon macrodactylus* inhabits more saline waters than *P. longirostris*, while the opposite is observed in the Guadalquivir estuary (González-Ortegón et al. 2010). In fact, the comparison of the salinity ranges where the introduced populations were recorded worldwide, shows a very heterogeneous use of habitats by *P. macrodactylus* (Figure 11). *P. macrodactylus* is clearly able to colonize systems with different salinities, from oligohaline to euhaline areas, which can be variable in time (estuaries) or not (Arcachon Bay). The range of salinity occupied by the Gironde population is close to the Guadalquivir population range. The opposite distribution observed compared to the native species *P. longirostris* comes from the fact that this native species inhabits more the oligohaline waters in the Gironde. *P. macrodactylus* and *P. longirostris* are both species with remarkable osmoregulatory capabilities as demonstrated by several studies (Born 1968; Campbell and Jones 1989; González-Ortegón et al. 2006). They are hyper-hypo-osmoregulators at salinities between 0 and 35, but it was observed that their field distributions were clearly biased toward lower salinity than their isosmotic points (González-Ortegón et al. 2006, 2010). The positioning of

P. macrodactylus in the gradient of salinity could depend only on the presence of other competitive species, in order to reduce inter-specific competition. For instance, the distribution of three species of mysids in the Guadalquivir was linked to the reduction of competition between them (Vilas et al. 2009). We think that the success of establishment by *P. macrodactylus* must be partially explained by its ability to exploit an array of habitats seldom occupied by the native species *P. longirostris*. This characteristic allowing the success of invasive species is emphasized by several authors (e.g. Hedgpeth 1957; Levine and D'Antonio 1999).

The estimated densities of both shrimps in the Gironde were significantly linked to the salinity, the temperature and the turbidity, for the separated sexes, which had never been tested to our knowledge. The salinity preferences vary significantly according to the sexes for both species, even if it is less pronounced for *P. macrodactylus* than for the native species. Thus, a spatial sexual segregation occurs in both populations: females inhabit less saline waters, as was shown for *P. longirostris* in Béguer et al. (2010a). This spatial sexual segregation could be linked to sexual dimorphism in body size (Ruckstuhl 2007), females being bigger than males for both species. The population densities are also significantly and positively linked to turbidity for both species. This preference for strong turbidities was shown for the *P. longirostris* population in the Seine (Mouny et al. 1998). The maximum turbidity zone is particularly rich in organic matter and shrimps could find favourable conditions for their feeding. Otherwise, some studies showed the role of turbidity as a refuge against predators for fish and for crustacea (Abrahams and Kattenfeld 1997; Maes et al. 1998). But, for the populations of the Guadalquivir, a negative relationship between densities and turbidity was shown for both shrimps (Cuesta et al. 2006). This difference with our findings could come from the range of turbidity which is much more restricted in the Guadalquivir (0-600 NTU) and more homogeneous throughout estuary than in the Gironde. Responses to temperature are similar for both sexes and species; the abundances decrease as temperature increases. This environmental factor varies monthly, and thus it must reflect several factors: population movement outside the survey area, recruitment (young of the year and individuals retained by the nets) and mortality. The tolerance to temperature variation could be greater for *P. macrodactylus* than *P. longirostris*. Two studies showed the strong ability of *P. macrodactylus* to

Figure 11. Salinity range where *Palaemon macrodactylus* was collected in various areas of introduction (according to this study, Ashelby et al. 2004; Béguer et al. 2007a; Buckworth 1979; Chicharo et al. 2009; Cuesta et al. 2004; d'Udekem d'Acoz et al. 2005; Gewant and Bollens 2005; Lavesque et al. 2010; Micu and Nia 2009; Spivak et al. 2006; Worsfold and Ashelby 2008). In black: range where the observed densities were highest.



survive at high temperatures, particularly in systems where temperature had artificially been increased (Buckworth 1979).

In our sampling area, the spatial overlap between *P. macrodactylus* and *P. longirostris* is strong enough and a significant spatial shift in the native species was revealed since the appearance of the exotic one. This upstream shift, towards less salty waters, was observed while the recorded salinity did not change significantly since 1992. However, a survey covering the period from 1979 to 2007, revealed a gradual increase in salinity in the intermediate part of the Gironde estuary (David et al. 2005; Delpech et al., pers. comm.). This salinity increase is commonly reported as a consequence of the global warming in estuaries (Shi et al. 2000) and it is explained by a decrease in rivers flow. It also may have been probably intensified by dredging in the navigation channel (David et al. 2005). Several changes were observed among the zooplanktonic and ichthyologic components. Thus, the upstream shift of the copepod population *Eurytemora affinis* was linked to increasing salinity and the associated shift of the maximum turbidity zone (David et al. 2007). The upstream shift of *P. longirostris* could also be explained by these reasons or by the trophic relationship between the shrimps and the copepods. Moreover, a progressive increase of the abundances of marine fish species was revealed in the intermediate part of the estuary, linked with the increase of salinity in this area (Delpech et al., pers. comm.). The expected

presence of *P. macrodactylus* in the downstream section that was not surveyed, before its detection in our samples, makes it difficult to discriminate between a direct effect of the exotic species on the shift of the native one and the effect of physico-chemical changes (salinity and temperature). In the Guadalquivir, a significant distributional shift was also revealed and indeed linked to salinity increase rather than to the exotic species effect (González-Ortegón et al. 2010). Our survey indicates strong monthly variations with horizontal movements of both populations, and a weaker spatial overlap during summer. The extended survey in 2007 shows that *P. macrodactylus* is almost absent from the intermediate part of the estuary in July and August, and occurs in very weak densities in the most downstream part. Additional samples collected in July 2007 on the rivers Garonne and Dordogne (see Figure 1), at a distance from the sea of around 125 km, showed an absence of *P. macrodactylus* upstream and strong densities of juveniles' *P. longirostris*. This confirms that the *P. macrodactylus* population range extends beyond our survey area, likely towards the more saline waters downstream.

Palaemon macrodactylus appears to have better reproductive traits than the native resident species

In the Guadalquivir, González-Ortegón et al. (2010) observed a higher proportion of juveniles in the population of the exotic species than in that of the native *P. longirostris*, and they

suggested a higher reproductive effort or success for *P. macrodactylus*. Our study shows a greater reproductive potential for *P. macrodactylus* than for *P. longirostris* in the Gironde estuary. Firstly, we showed a higher potential fecundity for the exotic species: *P. macrodactylus* produce more eggs than *P. longirostris* for same sizes. The fecundity of *P. macrodactylus* in the Gironde seems to be similar with the population of origin in Japan where the number of eggs produced varies between 300 and 3000 according to the individual female size (Omori and Chida 1988b). In Japan, ovigerous females reach a larger size of 17 mm CL which explains the greater number of eggs. In the Gironde, the mean number of eggs produced by *P. macrodactylus* could be underestimated because of the generally smaller size for the ovigerous females sampled. Indeed, our data showed a similar size at the onset of maturity for both species. So the biggest females of *P. macrodactylus* may not be correctly represented in our samples. This assumption is supported by observations of bigger females in the downstream part of the estuary which is usually not sampled (unpublished data). Moreover, laboratory work on *P. macrodactylus* showed that this species is able to reproduce several times (5-6) in a year (Omori and Chida 1988a, b) while the maximum number for *P. longirostris* would be two reproductions a year (Aurousseau 1984). Secondly, the relative proportion of *P. macrodactylus* larvae is very high (53% of stage V larvae) compared with adult stages (20% in 2007). The exotic larvae are very frequent and may represent up to 100% of the collected *Palaemon* larvae depending on the sampling month. This is confirmed by the higher proportion of juveniles for *P. macrodactylus* in the 2007 sampling.

Eggs produced by *P. macrodactylus* are smaller than those produced by *P. longirostris*, and this is linked to the greater batch fecundity of the exotic species. Smaller eggs could be both advantageous as it increases larval dispersal (Bauer 1991) and detrimental as it increases larval mortality, because of accessibility to a greater number of predators (Grahame and Branch 1985).

Other potential advantages of Palaemon macrodactylus versus P. longirostris

P. macrodactylus would be less likely captured in fisheries than the native species, mainly because of its location further downstream in the Gironde

estuary. Indeed, *P. longirostris* is traditionally fished mainly in the upstream part of the estuary and in the river parts Garonne and Dordogne (Girardin et al. 2008) where *P. macrodactylus* is weakly represented. Samples collected from commercial fishermen during their 2005 and 2007 fishing seasons show that approximately 95% of the collected shrimps belong to the native species *P. longirostris* (Béguer, unpublished data). Such a situation could however arise in the case of the geographical expansion of the exotic species. Moreover, a nuclear power plant, located in the intermediate part of the estuary (Figure 1), pumps shrimps into its cooling circuits on a daily basis resulting in some mortality. The proportion of *P. macrodactylus* captured by the plant in 2007 compared with *P. longirostris* is weaker, particularly in summer (Béguer et al. 2007b). It thus seems that in the Gironde *P. macrodactylus* is located in an area where it is relatively protected from human impacts (i.e. a type of refuge area). This is doubtless an important advantage for the exotic species.

Other studies in various localities revealed that *P. macrodactylus* could have other advantages over the native resident species. A better resistance to anoxic conditions was demonstrated (González-Ortegón et al. 2010). And in the Gironde estuary, anoxic events are frequent and occur mainly in the maximum turbidity zone which characterizes this estuary (Heip et al. 1995). Moreover some authors noticed that *P. macrodactylus* was particularly abundant in strongly polluted waters (d'Udekem d'Acoz et al. 2005; Spivak et al. 2006). Because of the similarity of its diet with the native species, *P. macrodactylus* could also compete for food with *P. longirostris*, in case of limited resources (González-Ortegón et al. 2010). In Australia, *P. macrodactylus* is qualified as an opportunistic feeder, which could even devour each other when in closed confinement (Buckworth 1979).

However, similarly to the native species, the population of *P. macrodactylus* in the Gironde, is strongly affected by morphological anomalies (about 24% of the examined shrimps in 2007) whose origins still remain unknown, though pollutants are one of the most likely causes (Béguer et al. 2008; Béguer et al. 2010b). These anomalies are detrimental to individual fitness (Béguer et al. 2010b) and thus could slow down the progress of the exotic species in the Gironde compared to other localities where the problem was not recorded.

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Supplementary material

The following supplementary material is available for this article.

Appendix 1. Total number of collected *Palaemon macrodactylus*.

Appendix 2. Salinity range (PSU, min–max) at sampling stations.

Appendix 3. Temperature range (°C, min–max) at sampling stations.

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